

2. Phytoplankton and Primary Production

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Background/Data Sources

Biomass

The broad-scale patterns in the spatial and seasonal distribution of phytoplankton biomass in the NEUS Ecosystem were described by O'Reilly and Zetlin (1998). These patterns were derived from 57,088 measurements of chlorophyll *a* made during 78 NEFSC MARMAP (Marine Resources Monitoring, Assessment, and Prediction Program) surveys conducted between 1977 and 1988. Additionally, we have developed a comprehensive time series of surface chlorophyll concentration for the NEUS based on SeaWiFS (Sea-viewing Wide Field-of-view Sensor) ocean color data collected since September 1997.

Production

Phytoplankton primary productivity measurements (^{14}C uptake rate) made during MARMAP surveys between 1977 and 1982 revealed that the Northeast shelf is among the most productive shelf ecosystems in the world (O'Reilly *et al.* 1987). While the *in situ* ^{14}C uptake method provides precise estimate of primary productivity, this method is expensive and labor-intensive, and therefore it is difficult to obtain sufficient spatial and temporal coverage to assess annual variability and long-term trends. At present, combining remotely-sensed data from satellites with productivity algorithms (Campbell *et al.* 2002) represents the only feasible method for resolving seasonal, annual, and climate-related variability of primary productivity throughout large marine ecosystems.

Quantitative Approach for Biomass Estimates

Estimates of standing stocks of phytoplankton biomass in the water column were based on chlorophyll *a* (Chl) concentrations and two approaches. The first approach used MARMAP vertical profiles of chlorophyll *a* pigment which were vertically integrated over the water column to a depth of 75 m (or bottom if $< 75\text{m}$) to yield mg Chl m^{-2} . Vertically-integrated chlorophyll (mg Chl m^{-2}) was averaged by standard stations/tiles (O'Reilly and Zetlin 1998) and by six bimonthly seasons. The annual mean (mg Chl m^{-2}) was computed for each station/tile from the six seasonal means. The annual means for each station/tile were then weighted by the area of each tile to generate the average phytoplankton standing stock (mg Chl m^{-2}) for the GOM (Gulf of Maine), SNE (Southern New England), GB (Georges Bank), and MAB (Mid-Atlantic Bight) regions.

The second approach used remotely sensed estimates of near surface Chl from 1,450 high-resolution SeaWiFS scenes of the region and the vertical profile model of Morel and Berthon (1989) to derive mg Chl m^{-2} for the euphotic layer from surface estimates. For these analyses, satellite data were processed according to the methods of Fu *et al.* (1998) and were mapped using a standard projection with an image size of 1024×1024 pixels and a resolution of $1.25 \times 1.25 \text{ km}$ per pixel. Annual mean integral chlorophyll (mg Chl m^{-2}) values for each pixel

were constructed from monthly means, and these were averaged to yield regional estimates of phytoplankton standing stocks (mg Chl m^{-2}).

Biomass Results

Table 2.1 compares estimates of phytoplankton biomass made by vertically integrating *in situ* data from MARMAP surveys with those based on SeaWiFS satellite estimates in Table 2.1. Since the SeaWiFS/Morel and Berthon Model estimates represent integral stocks in the euphotic layer and the MARMAP estimates are integrated standing stocks in the upper 75 m of the water column, we expect the latter estimates to be greater than the former. The MARMAP estimates are slightly higher than the satellite model-based estimates in the GOM but significantly higher in the other three regions.

Quantitative Approach for Estimates of Production

The Vertically Generalized Productivity Model (VGPM, Behrenfeld and Falkowski 1997) was used to estimate primary production. The VGPM incorporates remotely-sensed estimates of surface chlorophyll concentration and photosynthetically active radiation (PAR) from SeaWiFS and sea surface temperature (SST) from the NOAA AVHRR sensor (Advanced Very High Resolution Radiometer). In the VGPM, the optimal rate of productivity ($P_{b_{\text{opt}}}$: optimal water column carbon fixation [$\text{mg C } \{\text{mg chlorophyll } a\}^{-1} \text{ h}^{-1}$]) is modeled as a 7th order polynomial function of SST. In our application of the VGPM, which we designate VGPM2, the relationship between $P_{b_{\text{opt}}}$ and SST follows the exponential relationship by Eppley (1972), as modified by Antoine *et al.* (1996). A trial of the VGPM, VGPM2 and three other productivity models revealed that the VGPM2 yielded the best agreement with the MARMAP seasonal productivity cycle for the NEUS Ecosystem (O'Reilly and Ducas 2004) (Figure 2.1).

Daily VGPM2 estimates of primary production were computed for the 1998-2000 period using chlorophyll and PAR data from 1,450 high-resolution SeaWiFS scenes and SST data from 3,743 high-resolution nighttime AVHRR scenes of the Northeast U.S. SeaWiFS chlorophyll and PAR data were processed with SEADAS (Fu *et al.* 1998) and AVHRR SST was processed by NOAA CoastWatch using the MCSST algorithms (Multi-Channel Sea Surface Temperature). Satellite data were mapped using a standard projection with an image size of 1024 x 1024 pixels and a resolution of 1.25 x 1.25 km per pixel.

Phytoplankton Production Results

The generalized annual cycles of phytoplankton primary production for the four regions of the NEUS Ecosystem are illustrated in Figure 2.2. The annual mean primary production for each region is provided in Table 2.2.

Inputs to network models are usually in the form of organic carbon, calories, nitrogen, phosphorus, or wet weight. For this exercise, inputs to the network models were standardized to wet weight. Conversion of phytoplankton biomass and primary production from chlorophyll and carbon, respectively, to wet weight used factors provided in Table 2.3. The resulting GOM phytoplankton biomass value used in EMAX was $20.11 \text{ g wet wt m}^{-2}$. The net production value used in EMAX for the GOM was $3281.5 \text{ g wet wt m}^{-2} \text{ yr}^{-1}$, while the gross production was $4101.9 \text{ g wet wt m}^{-2} \text{ yr}^{-1}$. These wet weight estimates are derived assuming that organic carbon is

50% of the dry weight and the dry weight is 20% of the wet weight for phytoplankton, resulting in an overall conversion factor of 10 mg wet weight:mg carbon (Table 2.3). This is less than the 32.26 mg wet weight:mg carbon value used by Heymans (2001) (who assumed 3.23 mg dry weight:mg C and 10:1 wet weight:dry weight) for input to their model. Other studies employing the Ecopath model, such as that of Dalsgaard and Pauly (1997), used a conversion factor of 10 mg wet weight:mg carbon, within the range for algal weight:carbon indicated by Strickland (1966) in Table 2.3.

It should be noted that there is some confusion in the literature regarding the appropriate conversion factor to convert phytoplankton organic carbon to wet weight. It is worthwhile to quote Strickland's distinction between algal weight and wet weight (1966, p.15):

Two "wet weights" must be recognized, the true wet weight of the cells themselves with no extraneous water and the experimental wet weight obtained after draining the cells in some standard manner. The first weight is obtained from algal cell volumes, as measured microscopically, and a specific gravity value which, for all practical purposes, may be taken as unity. To avoid confusion this quantity should be called, simply, algal weight. The experimental "wet weight" will vary considerably according to the technique employed and will rarely, if ever, be less than twice the true algal weight, due to the presence of interstitial water. The confusion of these two weight figures by some authors has caused serious errors when computing, for example, chlorophyll:carbon ratios from cell volumes.

From the foregoing, it appears that the 10-12 mg algal weight:mg C is the most suitable factor for estimating phytoplankton biomass as "wet weight".

The EcoNetwrk software requires estimates of gross production. Conversion of primary production values for input to EMAX assumes that our estimates of primary production based on the VGPM2 and ¹⁴C methods represent net primary production and that net primary production and phytoplankton respiration are respectively 80% and 20% of gross primary production. Marra and Barber (2004) estimated daily plankton respiration as twice the dark uptake of carbon-14, where the dark uptake averaged 20-25% of the uptake during the light. Gross primary production can be calculated directly using the oxygen change method over a 24 hour period with light and dark bottles. Marra and Barber (2004) found good correlation between their carbon-14 estimate of phytoplankton respiration and the respiration from the oxygen change method during the North Atlantic Bloom Experiment (NABE). During this experiment the heterotrophic and phytoplankton respiration contributed equally to the total water column respiration. For comparison, Duarte and Cebrian (1996) estimate that phytoplankton respiration is 35% of gross primary production.

We assumed that the percent extracellular release (PER) of dissolved organic carbon by phytoplankton is 15% of the net primary production, based on ¹⁴C-uptake results from O'Reilly *et al.* 1987 (Table 2.3). For comparison, Nagata (2000) reported PER values ranging from 5%-30% and an average value of 11.3% for samples from the Gulf of Maine.

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Table 2.1. Integrated water column chlorophyll *a* concentration (Chl mg m⁻²) for the Mid-Atlantic Bight (MAB), Southern New England (SNE), Georges Bank (GB) and Gulf of Maine (GOM) regions of the Northeast U.S. Continental Shelf Ecosystem. (MARMAP data represent the vertically integrated chlorophyll to 75 m or bottom if less than 75 m; SeaWiFS - Morel and Berthelon estimates represent integrated chlorophyll over the euphotic layer.)

| Region | MARMAP 1977-1987 | SeaWiFS - Morel and Berthelon Model 1998-2000 |
|--------|---------------------|--|
| MAB | 61.80 | 50.11 |
| SNE | 71.34 | 51.18 |
| GB | 77.36 | 49.43 |
| GOM | 52.73 | 50.29 |

Table 2.2. Mean phytoplankton primary production (g C m⁻² d⁻¹) based on the SeaWiFS data and the VGPM2 model.

| Region | Primary Production 1998-2000 |
|--------|------------------------------------|
| MAB | 1.165 |
| SNE | 1.026 |
| GB | 0.900 |
| GOM | 0.900 |

Table 2.3. Phytoplankton conversions/comparisons.

| Quantity | EMAX | Reported Values | Reference |
|-------------------------------|------|-------------------------|--|
| mg C:mg Chl | 40 | 30 30 30 | Strickland 1966 Epply 1968 Banse 1977 |
| mg dw:mg C | 2 | 2 | Strickland 1966 |
| mg algal weight:mg dw | 5 | 5 | Strickland 1966 |
| mg wet weight:mg C | 10 | 32.26 10 16 10 | Heymans 2001 Dalsgaard & Pauly 1997 Walsh 1981 Bundy 2004 |
| mg algal weight:mg C | | 6.7-11.1 | Strickland 1966 |
| mg wet weight:mg Chl | 400 | 500 | Strickland 1966 |
| Respiration:Gross PP | 0.20 | 0.354 0.17-0.3 | Duarte & Cebrian 1996 Cloern <i>et al.</i> 1995 |
| Net PP:Gross PP | 0.80 | | |
| Percent Extracellular Release | 15% | 15% 11.3% | O'Reilly <i>et al.</i> 1987 Nagata 2000 |

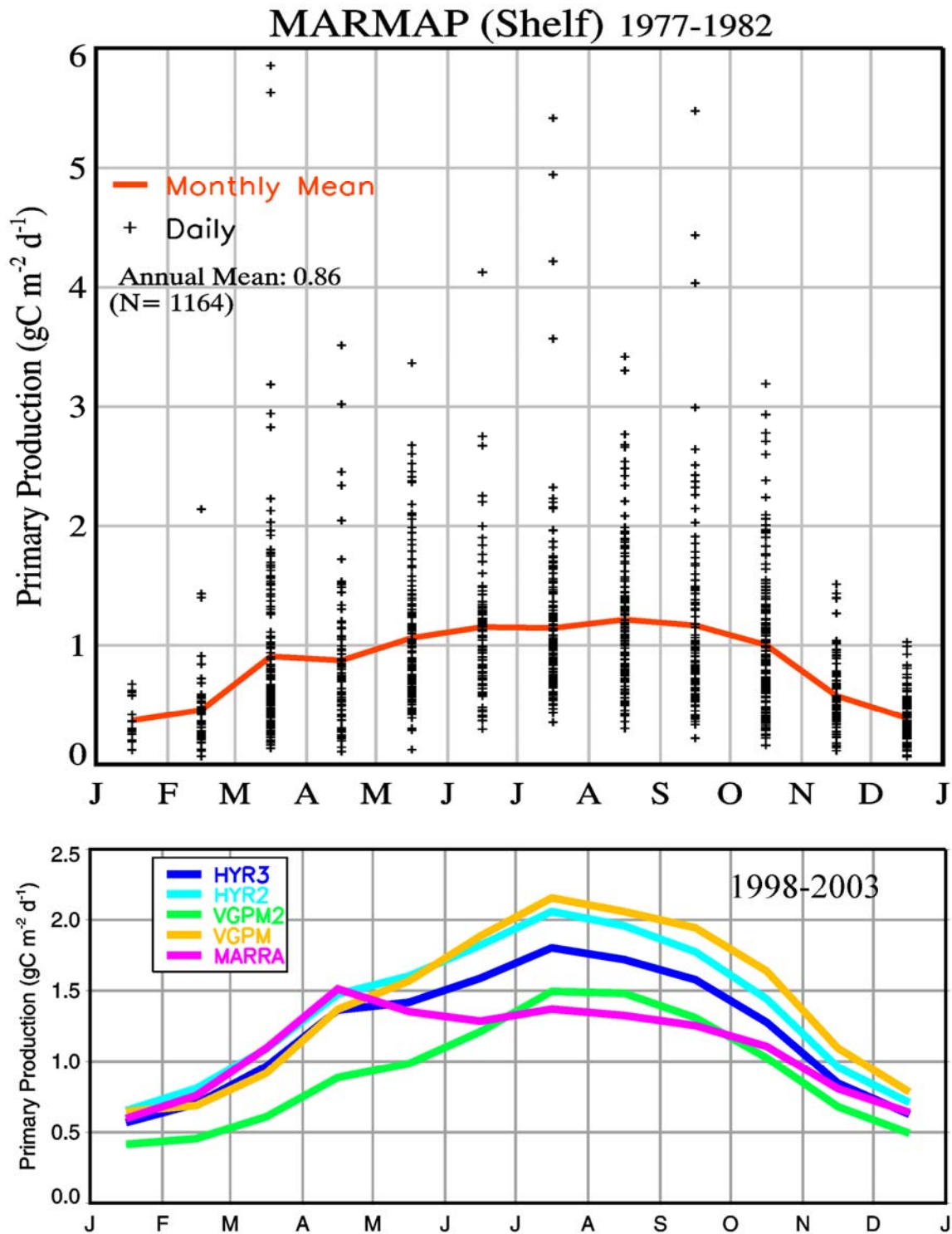


Figure 2.1. Upper panel: The annual primary production cycle for the Northeast U.S. Continental Shelf (MARMAP 1977-1982). Lower panel: Annual primary production cycle derived from satellite data (1998-2003) and productivity models (VGPM - Behrenfeld and Falkowski 1997; VGPM2 - see methods; MARRA - Marra *et al.* 2003; HYR2, HYR3 - Howard and Yoder 1997).

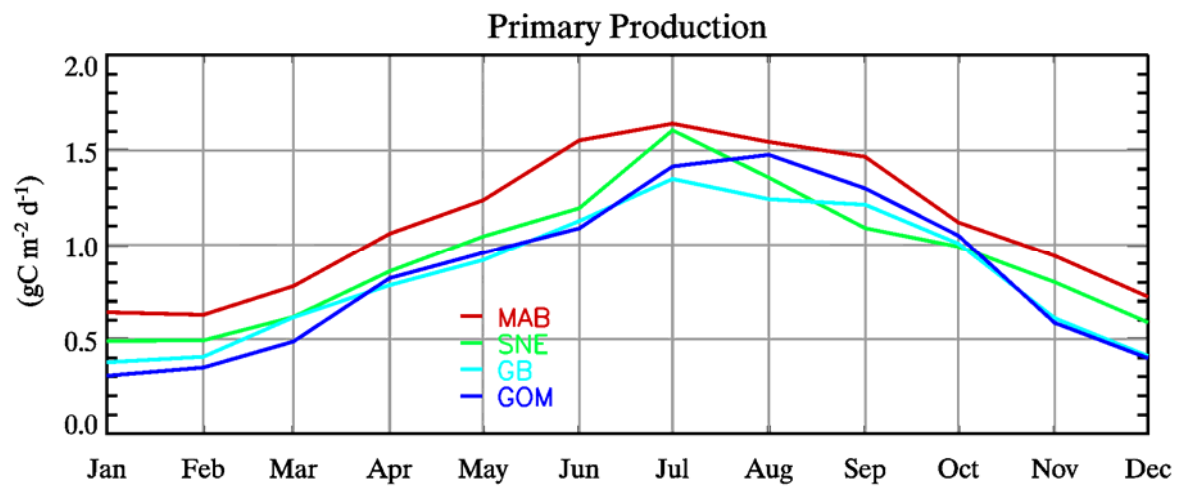


Figure 2.2. Annual cycle of primary production ($\text{g C m}^{-2} \text{ d}^{-1}$) for the Mid-Atlantic Bight (MAB), Southern New England (SNE), Georges Bank (GB) and Gulf of Maine (GOM) regions (1998-2000).